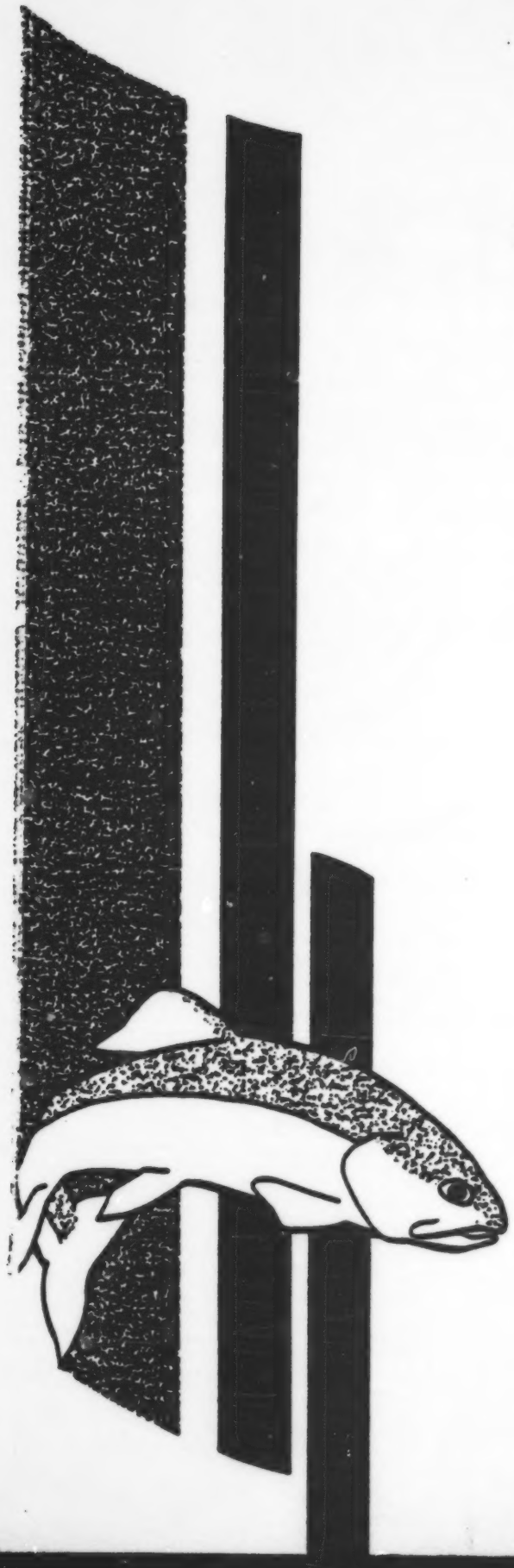

Kootenay Lake Fertilization Response Model

by

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PREFACE

This publication is the written summary of the Kootenay Lake Workshop, held at the Fisheries Centre, UBC, on February 20-22, 1991. Planning for the workshop began in late October, 1990, invitations were sent out in November, 1990, and the basic model structure was developed during December, 1990 to February, 1991.

Due to the brief time period between initial conception and the actual workshop, invitations were sent to a selected group of scientists, biologists and technicians who had been involved in similar studies or previous studies on Kootenay Lake, expressed interest in conducting future research on Kootenay Lake or were involved in the management of the recreational fishery on Kootenay Lake.

The list of participants was as follows:

Name	Organization
Harvey Andrusak	Fisheries Branch, MOE
Ken Ashley	Fisheries Research, MOE
Dr. Ed Carmack	Institue of Ocean Sciences, DFO
Joe DiGisi	Fisheries Centre, UBC
Colin Gray	NWRI, Environment Canada
Dr. Ken Hall	Civil Eng./Westwater Research, UBC
Dr. Paul Hamblin	NWRI, Environment Canada
Jeremy Hume	Cultus Lake Salmon Research Lab, DFO
Dr. Tom Johnston	Fisheries Research, MOE
Josh Korman	ESSA Inc.
Dr. Peter Larkin	Fisheries Centre, UBC
Dr. Dave Lasenby	Dept. of Biology, Trent University
Pete Law	Fisheries Branch, MOE
Dr. Greg Lawrence	Civil Engineering, UBC
Dr. Dave Levy	Levy Research Inc.
Bob Lindsay	Fisheries Branch, MOE
Earl MacIsaac	West Vancouver Laboratory, DFO
Brian Marotz	Montana Dept. of Fish and Wildlife
Al Martin	Fisheries Branch, MOE
Dr. Tom Murphy	NWRI, Environment Canada
Dr. Rick Nordin	Water Management Branch, MOE
Dr. Tom Northcote	Fisheries Centre, UBC
Eric Parkinson	Fisheries Research, MOE
Chris Perrin	Limnotek Research and Development
Dr. John Post	Fisheries Centre, UBC
Bruce Reiman	Idaho Fish and Game
Dr. Wilhelm Ripl	Technical University of Berlin
Joel Sawada	Fisheries Centre, UBC
Pat Slaney	Fisheries Research, MOE
Hugh Smith	B.C. Hydro
Dr. Carl Walters	Fisheries Centre, UBC

ABSTRACT

Walters, C., J. DiGisi, J. Post, J. Sawada. 1991. Kootenay Lake fertilization response model. Prov. B.C. Fish. Manage. Rep. No. 98:36p.

This report describes a computer simulation model developed to make predictions about the response of Kootenay Lake plankton and fishes to restoration of higher nutrient loadings. The model was developed using the Adaptive Environmental Assessment (AEA) workshop process, where a team of scientists with programming experience works with an interdisciplinary participant group of scientists and managers to translate the ideas, data, and policy concerns of that group into a working model for quantitative prediction. While the ultimate aim of the AEA process is to produce useful models for management, the initial aim in the workshop development is to clarify research priorities by directing attention to processes that are key to the model predictions but are difficult to quantify, to discrepancies between historical data and model predictions, and to alternative hypotheses that would give the same predictions.

The model appears to give credible quantitative predictions of basic nutrient dynamics and budgets (phosphorus inputs, outputs, horizontal and vertical transport, epilimnetic concentration patterns, responses of concentration to fertilization). However, there are major uncertainties in the model relationships that translate nutrient concentrations into predictions of phytoplankton and grazing zooplankton production, the utilization of zooplankton production by Mysis relicta and kokanee salmon (Oncorhynchus nerka), and the effect of changing kokanee growth rates and abundance on the interaction between kokanee and Gerrard rainbow trout (Oncorhynchus mykiss).

With the best available parameter estimates, the model "reconstructs" recent population declines in kokanee abundance as a combined effect of reduced food availability (on growth, fecundity, and time spent in sizes vulnerable to trout predation) and depensatory predation by trout. While the calculations attribute the reduced food availability partly to reductions in nutrient loading to the lake, the main impact is due to competition with Mysis for grazing zooplankters, particularly Daphnia. The model does not predict favourable responses of kokanee to lake fertilization; instead it predicts that fertilization will mainly enhance Mysis abundance and hence possibly even hasten the kokanee decline. Further, calculated predation rates by Gerrard trout are presently high enough to cause further kokanee declines, and search efficiencies by the trout are high enough to cause even higher mortality rates, so the kokanee may soon be unable to recover even if their growth rates are substantially enhanced by fertilization.

Thus it appears that the key uncertainties now are about how the zooplankton community (grazer species and size composition, Mysis) will respond to fertilization. At least four processes were identified that may counter the pessimistic baseline prediction that fertilization will enhance Mysis to the detriment of kokanee: (1) cannibalism preventing further Mysis increase; (2) increased export of Mysis over the West Arm sill under fertilized conditions, (3) increases in predation on Mysis by kokanee and other fishes; and (4) reduced relative importance of Mysis predation on early spring development of grazing zooplankton populations, under more fertile conditions. One or more of these processes apparently does operate in Kennedy Lake, where K. Hyatt and K. Cooper have measured positive responses of both Neomysis and fish to fertilization.

All indications from the model are that the kokanee are now caught in a squeeze between competition and predation that will result in collapse of the kokanee population (and hence the prized Gerrard stock) if no action is taken soon to control either one or both sides of the squeeze. Control of predation could not easily be accomplished by reduction in the Gerrard stock, due to its high recruitment rate per spawner, even if such reductions were politically feasible. Control of other predators is likely impractical for the same reasons. Hence it appears that the best management options are those related to kokanee productivity and competition with Mysis.

We conclude that it is still worthwhile to conduct a major fertilization experiment in the lake. It will be particularly critical during this experiment to closely monitor responses of Mysis (abundance, size, distribution, export to West Arm), grazing zooplankton (seasonal abundance, size distributions), growth of kokanee, and characteristics (size, number) of kokanee appearing in the stomachs of major predators - Gerrard trout, dolly varden (Salvelinus malma).

The situation with kokanee is now desperate enough, and the risk of its recovery being jeopardized by Mysis is high enough, that extreme options should now be considered to reduce Mysis abundance. These options include introduction of Mysis predators (such as deep water sculpin), use of bubblers or hydrodynamic oscillations to push Mysis toward the surface near the West Arm sill, and use of high fertilizer loads near the sill to reduce water clarity and induce Mysis to spend more time near the water surface (where they are vulnerable to export over the sill).

INTRODUCTION

This report summarizes the results of an Adaptive Environmental Assessment (AEA) workshop conducted in February 20-22, 1991 to produce an analysis of the possible effects of fertilization on the Kootenay Lake pelagic ecosystem. The basic concept of AEA workshops is to have a participant group of scientists and managers work with a modelling team to produce a working simulation model of the target system or problem (Holling 1978; Walters 1986). The simulation model acts as a focus of communication among specialists, and as a device to test whether conceptual models and data provided by the workshop participants are in fact adequate to make credible predictions when integrated in precise quantitative terms by the simulation program.

For Kootenay Lake, the AEA modelling process proceeded in two stages. First, a UBC modelling team (report authors) met with Fisheries Branch research and management biologists over the period November 1990-January 1991, to set basic terms of reference (policy options, variables to be considered) for the model and to produce a first working version of the simulation program. This program was then used as a "straw man" or starting point for further model development and refinement during the February workshop. Here we describe the final working model resulting from the workshop.

THE GENERAL MODEL STRUCTURE provides an overview of the model structure, space and time scales used in the various submodel calculations, data used to test the model predictions, and specific policy options now included in the simulation program for further policy exploration. Further detail on the submodels and policy options is given in the DESCRIPTION OF SUBMODELS AND LINKAGES, and the MODEL USERS GUIDE provides a general users guide to the program. KEY UNCERTAINTIES IN MODEL PREDICTIONS OF RESPONSE TO FERTILIZATION are summarized and RESEARCH PRIORITIES are recommended to help resolve these uncertainties in conjunction with a large scale fertilization experiment on the lake.

GENERAL MODEL STRUCTURE

The general aim of the AEA model is to simulate long term (30+ year) changes in plankton, kokanee, and Gerrard trout populations in response to changes in lake fertility associated with phosphorus loading. The model also tries to simulate effects of strategic fisheries management options such as varying exploitation rates and enhancement of spawning success through technologies such as spawning channels. The model is provided with historical inputs (nutrient loadings, water flow patterns, changes in kokanee spawning habitat) for the baseline simulation period 1960-89 so that its predictions can be compared with various data time series available for that period (and provided to the simulation program for graphic display along with the model predictions); it can

extend the predictions out to the year 2010 using assumed input patterns provided by the model user.

The model is programmed in Quickbasic (Microsoft Corp. TM), using a "front end" or skeleton program structure developed at UBC to facilitate interactive simulation and game playing. The front end provides the user a series of menus and spreadsheet-like displays for changing model parameters and policy options, saving and retrieving parameters and results from files, and displaying the model results and data in various graphical formats (maps, time series plots) as each simulation proceeds. Complex scenarios can be developed by interrupting the simulation at various times to make changes in various policy parameters. The model will run on any IBM compatible PC with VGA graphics adapter; it requires about 30 s to do a 30 yr scenario on 20mh 80386 systems with 80387 math coprocessors. Copies of the model and data files are available on 720k 3-1/2" diskette from the authors.

Submodels and Variables Considered

The simulation program has five basic submodels for key components of the Kootenay Lake production system:

-nutrient budgets (inflows, mixing processes, losses)
-phytoplankton/grazing zooplankton production
-Mysis energetics and population dynamics
-kokanee energetics and population dynamics
-Gerrard energetics and population dynamics.

The nutrient budget submodel generates space/time patterns of phosphorus concentration, which in turn are used (in part) to drive the phytoplankton/grazing zooplankton predictions (which feed back on the nutrient budget calculations through impacts of the plankton on sinking rates of phosphorus from the lake epilimnion). The grazing zooplankton predictions are then used to predict feeding and growth rates of Mysis and kokanee, and these feeding rates then feed back to influence the zooplankton abundance and type (cladoceran, copepod) composition. The Mysis and kokanee growth predictions are used along with other information to predict basic population dynamics of these species (age composition, fecundity, survival, seasonal life history events). Abundance and size composition of the kokanee population is used to predict Gerrard trout feeding and growth rates, and mortality impacts on the kokanee. Gerrard growth predictions and other information (spawning, early growth, harvest rates) are used to predict changes in the Gerrard population age and size structure.

A key emphasis in the overall model structure is to represent key interactions surrounding kokanee salmon. On the one hand, these fish are facing a declining food supply and declining growth rates due to plankton production and perhaps competition with Mysis (Northcote 1972, 1973; Lasenby et al. 1986). On the other hand,

reduced growth makes them more vulnerable to predation by the very efficient Gerrard rainbows, which have been stable or even increasing in abundance in recent years due to changes in hatchery programs and protection of spawning habitats. The kokanee is thus caught in the middle of two relatively successful "restoration" efforts, one aimed at reducing eutrophication problems and the other aimed at protecting the Gerrard stock (Korman et al. 1990).

Computational Scales and Resolution

To capture the variety of ecological and physical processes that might be important to fertilization response, the model carries out calculations and predictions on several spatial and temporal scales. These range from cubic meters of water and hourly or diurnal time scales for prediction of feeding behaviours of Mysis, kokanee, and trout, up to the whole lake over time scales of months and years for prediction of kokanee and Gerrard population dynamics.

The basic nutrient budget calculations are done on 2000 ha spatial grid cells (26 for the lake surface waters, same for hypolimnion waters) on a monthly time step, so as to represent seasonal variation along Kootenay Lake's main axes in nutrient concentrations and water exchanges. This spatial resolution also permits exploration of alternative fertilization policies such as riverine or point source additions, or fertilization of just the North Arm. Some very rapid nutrient dynamics, such as dispersal of nutrients from point sources due to wind-driven surface mixing, are represented by calculating "instantaneous" or equilibrium patterns that vary seasonally.

Phytoplankton and grazing zooplankton dynamics averaged for the whole lake epilimnion are simulated with a daily time scale or step in order to capture key seasonal interactions with plankton predators. In particular, we found it important to follow impacts of predation on grazer population dynamics early in the annual growing season, when predator:prey ratios are high and high predation rates may have a major impact on at least the type (cladoceran/copepod/rotifer) composition of the grazing community through the remainder of the growing season. Mysis, kokanee, and Gerrard energetics (feeding, metabolism, growth) are simulated on a monthly time step, averaged for the whole lake surface. At appropriate months each year, annual events such as spawning migrations and entry of juveniles into the lake are simulated, and population age structures are updated.

The only modelled events taking place outside the lake system (regional spatial scale) are (1) seasonal regulation of water flows due to the Duncan and Libby Dams; (2) seasonal loading of phosphorus into the Duncan and Kootenai Rivers; and (3) spawning and egg-fry survival of kokanee and Gerrards. The kokanee spawning migrations and egg/fry production are simulated for three spatial locations (Duncan, Kootenai, and Meadow Creek stocks).

Driving Variables and Comparison to Historical Data

To insure that the model can at least produce a credible reconstruction of recent historical changes in Kootenay Lake, we set it up to always run through a 1960-89 base period before making any predictions of future changes. Cumulative departures of model predictions from data over this base period then provide a warning about whether the current model parameter values and relationships have any hope of making a correct prediction about future changes. For the 1960-89 base period, we provide the model an input time series of water management regimes (regulation or natural seasonal flow pattern) for the Duncan and Kootenai Rivers, and a series of annual phosphorus loadings for these rivers (Daley et al. 1981; Korman et al. 1990).

We also simulate key events in the history of the kokanee populations, by removing and/or enhancing spawning habitat at appropriate years to represent losses due to dams and the construction of the Meadow Creek spawning channel. In the present draft of the model, we unfortunately have not been able to provide a similar time series of events that have influenced spawning and mortality of the Gerrard trout. Josh Korman and Chris Perrin provided a computer data base of nutrient, plankton, and fish annual data for the period 1972-89 (from Korman et al. 1990), and some monthly seasonal data for zooplankton populations for that same period. The annual data are read into the simulation program for plotting along with the model predicted values (the data are not used directly in the computations).

Policy Options Included

The program is set up to explore three main types of policy options: (1) changes in nutrient loading through manipulation of river concentrations and/or direct fertilization of the lake surface; (2) enhancement of reproductive success of kokanee and/or Gerrards outside the lake, through manipulation of spawning success and juvenile carrying capacities; and (3) changes in harvest rates (and sizes harvested) for kokanee and Gerrards. Policy options related to nutrient loading are represented in considerable detail, while the fish policy options involve only changes in crude, annual rates.

The model can also be used to explore various options for control of Mysis numbers, by varying Mysis mortality rates (to represent introduction of predators) and the vulnerability of Mysis to export over the West Arm sill. However, the model will not automatically account for any unintended side effects of such manipulations, such as competition between introduced predators and existing fishes or impacts of changing water clarity on fish feeding and the plankton production system.

DESCRIPTION OF SUBMODELS AND LINKAGES

The submodels described below are embedded in a simulation time loop over years and months within years. Most of the calculations described below are repeated for each month over the entire simulation period, except as noted for special cases where calculations are done on shorter (e.g., day) time steps or only once per year at times of particular key seasonal events such as spawning and graduation in ages of fish.

Each submodel is reviewed in a four-subsection format: (1) functional relationships and limiting factors considered; (2) predictions and sensitivity to key parameters; (3) uncertainties and alternative hypotheses; and (4) suggestions for future improvement. Mathematical notation and bookkeeping details are avoided, so as to highlight key assumptions and possible weaknesses. At several points in the review, we describe comparisons between submodel predictions and historical observations. The most important comparisons are shown in Fig. 1, which shows the PC screen display at the end of a baseline simulation run (1960-1989). The upper right side of the display (six graph "panels") shows annual data (dots) and annual simulation results (dashed lines).

Nutrient Dynamics and Primary Production

The model attempts to provide a fairly detailed space/time accounting of total phosphorus concentrations, to permit evaluation of various fertilization strategies such as riverine additions, lake point source additions, and additions to only the North Arm to set up a north/south experimental gradient in impacts. To allow such evaluations, the lake is divided into 26 surface (0-20 m) cells (2000 ha each) along the main lake axes; there is a hypolimnetic cell (20-100+ m) underlying each surface cell in the calculations.

Inputs to the submodel are water volume and phosphorus concentrations in the main river inflows (Duncan, Kootenai), and a space/month pattern of P fertilizer input. The basic result of the submodel calculations for each simulation year is a monthly pattern of total P concentration and total algal biomass over these 52 surface and deep water cells. Mean epilimnetic total P over the cells is calculated for use in the grazing zooplankton submodel, and monthly water volume transport rate over the West Arm sill is predicted for use in the Mysis submodel (as a component of mortality).

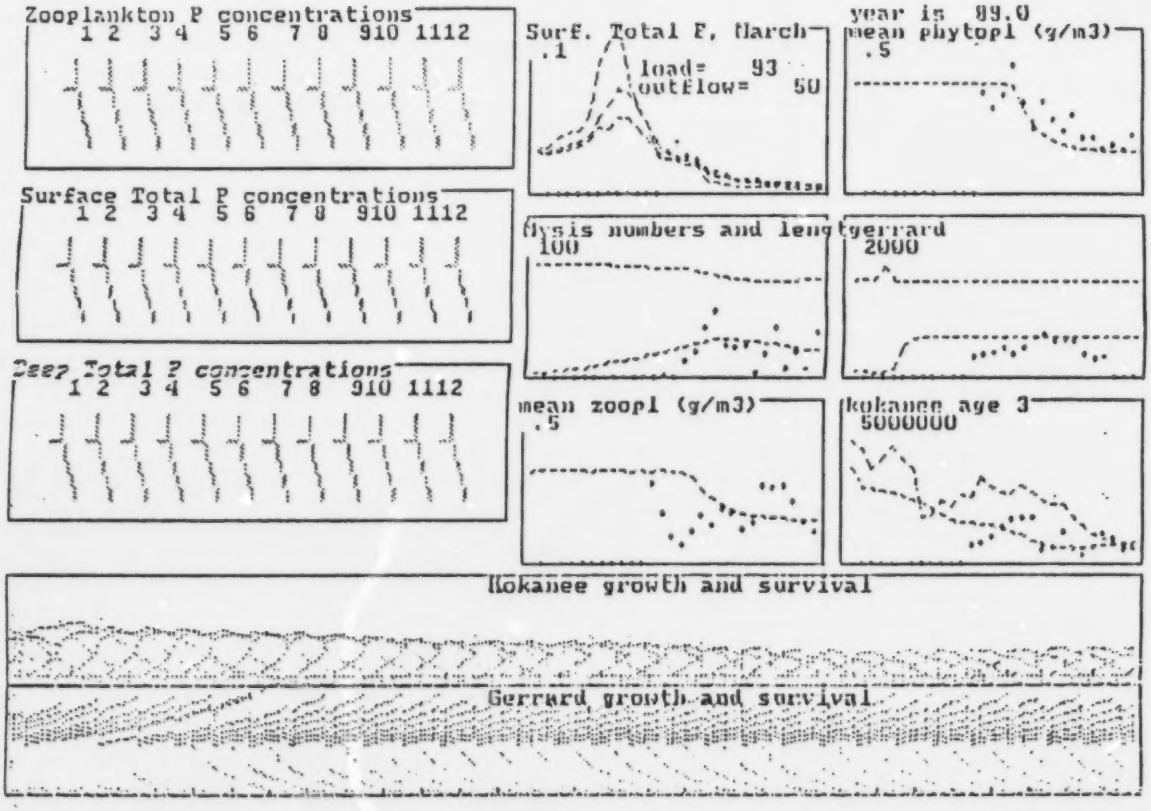

Figure 1. PC display screen at the end of a baseline simulation (1960-1989), showing information displayed by the model as it runs (the screen is updated every simulated month). The upper left part of the screen (three graph panels) show monthly (1=Jan. to 12=Dec.) maps of zooplankton and phosphorus concentrations along the main axes of Kootenay Lake. The upper right part of the screen (six graph panels) shows annual model results for some key indicators, and measured values (dots) for these indicators for simulation years 1972-89. Note that the observed surface Total P values for March are almost exactly aligned with the model predictions, so the observed values for 1976-89 do not show on the paper copy in the figure. The lower two graph panels (kokanee, Gerrard growth and survival) are updated monthly to show seasonal changes in body lengths and numbers for each cohort present in the population; on the PC screen, the growth and numbers curves are colour-coded to be easily read compared to the paper copy in the figure.

Functional Relationships and Limiting Factors

Phosphorus concentration in any cell is assumed to change due to direct fertilizer additions and to volume exchanges with adjacent cells (horizontal and vertical mixing, volume transport toward the outlet). The deep water cells are assumed to have only horizontal and vertical mixing components. Also, phosphorus moves into the deep cells due to particulate sinking from the surface, and from the deep cells into the sediments (as "permanently" bound P). Considering these processes, the concentration in cell i (p(i), i ordered from i=1 at Duncan inflow) is assumed to behave according to the simple differential equation:

$$dp(i)/dt=V(i-1,i)p(i-1)+V(i+1,i)p(i+1)+f(i)-[V(i,i)+s+b]p(i)+Mp'$$

where the V(.,.) are water volume exchanges (volume moving/volume present), f(i) is fertilizer addition, and s and b are sinking loss rates (s for surface cells, b for deep cells).

Deep water cells have an additional component s/Vp(i) for sinking additions from the surface cell above. The V(i,i) loss rates all include a component for vertical mixing with the cell below (or above for deep cells), and all cells have a gain Mp' for mixing with water having concentration p' in the cell above (or below). For North Arm surface cells, the V(i-1,i) have Duncan River discharge and horizontal mixing components, while the V(i+1,i) exchanges have only the horizontal mixing component; for South Arm cells, the V(i+1,i) volume exchanges include Kootenai discharge and horizontal mixing, while the V(i-1,i) represent only horizontal mixing.

The West Arm surface cells have V components for both Duncan and Kootenai river discharges, plus horizontal mixing components (except no horizontal mixing is assumed to occur across the West Arm sill). The V components due to river discharge are varied seasonally in the calculations (and the seasonal pattern can be set as a policy parameter, e.g., to re-establish seasonality of flows from the Duncan and Libby Dams), as are the vertical mixing rates.

For surface cells, the above differential equation has large enough V components to imply equilibration on a time scale of days or weeks rather than months. Therefore, we assume dp/dt=0 for these cells, and solve the resulting tridiagonal linear system for the equilibrium surface p(i) at any point in time when these concentrations are needed. Note that the surface p(i) will still vary over time, due to seasonal changes in the rate coefficients (V, s, M, f).

For deep cells, the time scale for reaching equilibrium is on order of months or years. Therefore, we solve the differential equations using a variable time step numerical algorithm, with a maximum time step of one month. Surface equilibrium concentrations

are recomputed as needed while the calculations proceed through the variable deep water time steps.

A key test of this computational algorithm was developed in the AEA workshop, and involved using it to simulate a conservative chemical property (conductivity) with a strong North-South gradient (Kootenai River input conductivity is double the Duncan input; Daley et al. 1981). The algorithm performed very well, and helped us to narrow the estimates of horizontal (wind) mixing velocities to between 0.5 and 2.0 km/day.

Mean monthly algal biomass is calculated for each cell as a sum of two components: grazeable and ungrazeable (large cell, colony). Grazeable biomass is assumed to remain near equilibrium with grazing rates (see section below), and ungrazeable biomass is assumed proportional to the total P concentration less P currently in grazeable algae and zooplankton biomass. This proportionality is assumed to break down for total P concentrations above 20 μg/L, when low N:P ratios would imply nitrogen limitation. The monthly proportionality constant for large algae was estimated empirically from chl A data for the lake, and essentially just represents a Vollenweider (1976) empirical model for prediction of algal biomass from phosphorus.

The sinking loss components sp(i) for surface cells are assumed to be proportional to total plankton (algae+zooplankton) biomass. Thus the simulated surface cells lose P less rapidly to sinking in winter, and when total P concentrations (and hence biomasses available to create detrital material) are lower.

Predictions and Sensitivity to Parameters

The phosphorus budget model appears to give quite accurate predictions of spatial, seasonal, and long term (1960-1989) variation in surface and deep water P concentrations, when compared to data in Daley et al. (1981). In particular, it produces a very good fit to the historical time series of surface P measurements (Korman et al. 1990) indicating a long period of decline in surface concentrations following the abrupt reduction in P loadings in 1969-70. It attributes the long decay period (relative to what would be expected based on total volume exchange estimates for the lake) to relatively slow mixing of P from the large pool in deep water with the fast-moving surface waters that carry most of the river discharge. The algal biomass model also fits the data quite well, but this is not surprising since it is really just an empirical regression model based on the data.

Key model parameters in terms of fertilization policy predictions are the detritus sinking, vertical mixing, and horizontal mixing rate parameters. The sinking and vertical mixing parameters are important determinants of how long it takes for P added to surface waters to be lost to the hypolimnion, and how fast

the surface waters are recharged by mixing from the deep waters. Horizontal mixing rates are key to predictions about the efficacy of point-source fertilization options, and for evaluation of whether a strong north/south experimental gradient can be established by fertilizing only in the North Arm. Over a wide range of estimates of the mixing and settling parameters, the model suggests that such a gradient can indeed be established and maintained, at least during the summer months.

One interesting point is that we cannot make the model fit the historical data if we assume high net (permanent) loss rates of P to the sediment. Assuming loss rates above about 0.0002 of the total hypolimnetic P per day leads to predicted deep water and surface concentration declines much faster than observed over the 1970-80 period after inputs were reduced. Thus, the deep hypolimnion appears to be very efficient at remineralizing phosphorus settling from the surface waters; this is not surprising considering the depth of the lake and its high hypolimnetic oxygen concentrations. Note that efficient hypolimnetic regeneration of inorganic P does not imply that the lake only needs to be fertilized at long intervals (e.g., every two years). During the growing season, P is still lost rapidly from the epilimnion due to the sinking of particulates, and this loss needs to be replaced by frequent fertilization over each growing season even if the hypolimnion then accumulates substantial P over the long term.

Uncertainties and Alternative Hypotheses

There are modest uncertainties concerning mixing and settling rates. These can likely be resolved by tinkering with the model to make it fit historical data more precisely, by examining its parameter values in relation to the predictions of more detailed physical models of the lake, and by doing relatively simple experiments with detritus settling traps.

There is more important uncertainty concerning the biological fate of phosphorus. Given total P concentrations, we are not confident in the model predictions about the partitioning of algal uptake and production between grazeable and ungrazeable algal forms, and about the extent to which production rates of grazeable algal forms are limited by P even at the relatively low concentrations found in the lake today (see next section). Simple phytoplankton-zooplankton interaction models predict that no further increase in zooplankton production will occur once the system becomes fertile enough to support ungrazeable forms (Walters et al. 1987). Instead, all further increase in total P is predicted to just enhance biomass of the ungrazeable forms. More complex models that assume a progressive replacement of more grazeable and nutrient-efficient forms by less grazeable and inefficient forms lead to some predicted increase in zooplankton production with eutrophication, but this increase might be quite modest. The Kootenay Lake zooplankton data do not show a marked

decline in total biomass from the 1960's to the present, which could mean either that total production of grazeable algae has not changed very much or that the zooplankton community is limited by other factors (e.g., Mysis and kokanee predation).

An important point about the primary-secondary production predictions is that fertilization may increase production even if production rates of grazeable algae are now limited mainly by grazing rather than by phosphorus availability. The model predicts that under current loading patterns, the epilimnion will "run out" of P very early in each growing season, due to reduced recharge from the hypolimnion, lower than natural water flows during summer, and loss of P from the hypolimnion due to settling. Summer fertilization might offset these effects to produce a longer growing season (zooplankton biomasses available to fish remain high longer each season) even if much of the late season fertilizer additions contribute mainly to increased biomass of ungrazeable algal forms.

Suggestions for Model Improvement

The key need now in this part of the model is to look very closely at the predictions of primary production in relation to total P concentrations, and in particular at the productivity of algal forms that can be grazed by the zooplankton community. There is also a need to calibrate the P budget model more precisely with regard to the horizontal transport, winter vertical mixing, and particulate settling rate parameters.

Grazing Zooplankton Abundance

The basic objective in the grazing zooplankton submodel is to predict seasonal changes in the availability of food for Mysis and kokanee, averaged over the lake surface to reflect the substantial ability of planktivores to "average out" any local spatial variation through their movements. To accomplish this objective, we found it necessary to predict zooplankton changes on a one-day step in order to capture rapid transient responses early in the annual growing season. The grazing zooplankton biomass is represented as two components, cladocerans and copepods, which have grossly different population response rates and vulnerabilities to predation (Muck and Lampert 1984).

Cladocerans are assumed to have very rapid seasonal population growth, to practically disappear during winter, and to be very vulnerable to planktivores. Copepods are assumed to have relatively slow population growth rates (one or a few generations per year), to have relatively high overwinter survival rates, and to be much less vulnerable to Mysis and fish predation. Size and species distributions within these planktonic types are not considered in the calculations.

Functional Relationships and Limiting Factors

The seasonal dynamics of copepods and cladocerans are assumed to be closely coupled to the seasonal dynamics of grazeable algae. The coupled dynamics of these three variables, and effects of varying phosphorus concentration, are represented by the very simple differential equation model:

$$dA/dt = r(t)AF/(ks+F) - fcCl - foCo - sA$$

$$dCl/dt = [fc - mc - umcl - ukcl]Cl$$

$$dCo/dt = [fo - mo - umco - ukco]Co$$

where A is grazeable algal biomass, Cl is cladoceran biomass, Co is copepod biomass, and F is available phosphorus concentration (total P minus amount of P already in algae and zooplankton biomass: F=T-A-Al-Cl-Co where T is total P and Al is biomass of large algae from the submodel described above). For convenience in the accounting, A, Cl, and Co are all measured in phosphorus units (e.g., mg of phosphorus in cladoceran biomass per liter). Dry weight biomasses for predation rate calculations are then assumed to be constant multiples of the biomass measured as P (a conversion of 100:1 dry weight:phosphorus is assumed as a baseline).

The algal growth rate term r(t)AF/(ks+F) represents effects of photoperiod and nutrient concentration on algal growth. r(t) is a seasonally varying maximum daily growth rate based on light/temperature (Lehman and Sandgren 1985), and ks is a Michaelis constant for effect of free nutrient concentration on algal growth rate. We use r(t) values ranging from 0.3 to 1.2/day over the year, and as a baseline assume that ks=0.6 μg P/L.

The algal loss rate terms represent grazing losses by cladocerans (fcCl) and copepods (foCo), and sinking/senescence losses sA. The filtering rate parameters fc and fo for copepods and cladocerans represent the basic mechanism by which algal biomass (and production) is transmitted to the zooplankton community. Based on laboratory and field data, we chose to assume fc=fo=300 ml/μg zooplankton P/day (Buckingham 1978; Chow-Fraser and Knoechel 1985; Chow-Fraser 1986; Peters and Downing 1984). s is assumed to be around 0.2/day.

The biomass dynamics equations for copepods and cladocerans above each consist of a grazing input term (fcCl, foCo) that is also an algal loss rate, minus a series of loss terms. The terms mcCl and moCo represent "natural losses" (metabolism + excretion + non-predation mortality); these are set to 0.1/day for cladocerans and 0.05/day for copepods, and are not assumed to vary with season or temperature (Buckingham 1978). The predation loss rates (proportions of biomass per day) umcl and umco represent Mysis removals (see Mysis model below), and the proportional loss rates

ukcl and ukco represent predation by kokanee (see below).

To improve computational stability, we generally agree that the algal biomass remains near equilibrium, i.e., that production and loss rates quickly (time scale of a few days) achieve a balance whenever conditions (r(t), grazing, T) change. Thus we solve the algal rate equation for A each day, after setting dA/dt=0. Essentially the same predictions are obtained when the time dynamics of A are simulated, except that an unstable (and probably unrealistic) phytoplankton/zooplankton cycle appears when the system is very productive.

The biomass dynamics equations alone do not adequately account for annual cycles of abundance. In particular, they do not account for the various strategies that zooplankters have developed, such as resting eggs, to improve survival through the difficult winter period when little food is available yet major predators are still present. To model these life history effects, which can be very complex and species-dependent, we simply set a minimum biomass for each zooplankton type; biomass is reset to this minimum in any month for which the dynamic equations predict lower biomass.

This assumption in effect "reseeds" the system with a low biomass of new copepods and cladocerans throughout the year, which will then grow if food/mortality conditions permit. The zooplankton feeding rates also need to be constrained, to prevent unrealistically high biomass growth rates during periods of high algal abundance in early spring when nutrient concentrations are highest and zooplankton populations are still low. Upper limits on feeding rates per unit biomass (0.4/day for cladocerans, 0.1/day for copepods) were set in the model so as to give maximum daily population growth rates corresponding to maximum observed field growth rates in populations not subject to intense predation (UBC Research Forest Lakes).

Predictions and Sensitivity to Parameters

The basic biomass dynamics model with minimum biomass constraints appears to represent seasonal and interannual changes in copepod biomass quite well. It predicts a seasonal biomass peak in July as observed, a ratio of about 10:1 in the seasonal maximum and minimum biomasses, and a gradual decline through the 1970's and 1980's in the peak biomass and seasonal duration of high biomasses. Neither Mysis or kokanee predation is predicted to cause any severe "crashes" in the copepod biomass. The model "explains" the lack of major long term decline in copepod biomass with decreasing lake fertility as a consequence of the Michaelis constant for growth rate of grazeable algae in relation to phosphorus concentration: over most of the historical period, grazeable algal production in the model is limited by grazing (production close to the upper maximum rate r(t) times biomass, biomass held down by grazing).

The model is not so good at capturing observed changes in cladoceran biomass. It does generate the observed pattern of low cladoceran biomass relative to copepod biomass (Zyblut 1967), and the near disappearance of cladocerans during times of peak Mysis abundance in the 1970's and early 1980's. However, it does not correctly represent the observed seasonal pattern of cladoceran abundance, at least for the 1970's. It predicts peak cladoceran biomass in April and May, due to their relatively high potential for population growth early in each growing season, and a decline to near extinction by mid-summer each year. The available data suggest that spring "blooms" of cladocerans are not the regular pattern, and that biomass peaks occur in August and September instead. However, Zyblut (1967) reported Daphnia galeata mendotae present in June-August 1949, but not in 1964, and noted that the late summer biomass peak as of the mid-1960's consisted mainly of Diaphanosoma leuchtenbergianum. His results suggest that the model may even be underestimating the impacts of Mysis on Daphnia spring population development, and failing to capture the life history characteristics that permit summer development of species like Diaphanosoma.

The model predicts that predation mortality rates, especially by Mysis, should be particularly high early in the growing season (March-April) when the predators are starting to feed actively and the predator:prey ratio is high (At that time the zooplankton are just beginning to recover from their winter minimum caused by low algal production). It is this intense period of predation that causes the modelled cladoceran biomass to be very low for more recent years in the simulation, rather than reductions in lake productivity. The data showing lack of a spring cladoceran bloom do support this prediction of a spring "predation bottleneck", but it appears that we have failed to capture some mechanism by which at least some cladoceran production is realized late in the growing season. Perhaps this mechanism involves reduced predation on cladocerans during the midsummer period when mainly neonate mysids are present; neonates eat mainly rotifers (which we did not include in the zooplankton model).

The model predictions of seasonal population development, especially of cladocerans, are very sensitive to the values assumed for minimum biomasses. Increasing the copepod minimum results in extinction of cladocerans (copepods "take over" the available food supply too soon), and lowering the minima generally results in greater sensitivity of predicted seasonal biomass development to high predation rates early in the growing season. The predictions are also somewhat sensitive to the assumed maximum feeding/biomass growth rates, but we are reasonably confident about the maxima assumed in the model since there is a large body of empirical data on both maximum feeding rates and maximum spring population growth rates for grazing zooplankters.

Uncertainties and Alternative Hypotheses

There are two key uncertainties in the grazing zooplankton predictions: (1) is production of grazeable algae actually limited by grazing, or by availability of nutrients, especially late in the annual growing season? and (2) is cladoceran production currently limited by high predation rates as predicted by the model, or instead by reductions in algal productivity and associated competition with copepods? As it is currently parameterized, the model predicts little response of grazing zooplankton to fertilization, due to a combination of algal limitation and predation effects. The increases that it does predict (due mainly to increases in the length of the growing season) end up being translated into increased Mysis abundance and production rather than improved growth and survival of kokanee.

It is quite possible that fertilization will result in changes in grazing zooplankton size/species composition that are more favourable to kokanee than Mysis production. We have no way of predicting in advance how such changes might look, since there are many zooplankton species and life history patterns that might participate in the change. Based on historical experience with Kootenay Lake, there are no obvious candidates for response.

Suggestions for Model Improvement

The key need at this point is to examine the seasonal population ecology of the main grazing species in more detail, with a particular aim to understand how key cladoceran and copepod species deal with relatively high predation rates early in the growing season. Most likely the copepods get through this period mainly by having life history strategies with appropriate patterns of body size (e.g., early spring population consisting mainly of nauplii and small copepodite stages too small for kokanee, or larger adults that are less vulnerable to Mysis).

Another key need is to look in more detail at the types/sizes of algae actually used successfully by the grazing zooplankton community (Carpenter and Kitchell 1984). Our partitioning of algae into "grazeable" and "ungrazeable" is clearly too simplistic, especially in regard to questions about response to fertilization. While predation on larger zooplankton species may prevent the development of a zooplankton community capable of using much of the increased production of larger algal forms expected under fertilization, at least some of that increase may be usable by smaller species that use specialized feeding strategies (e.g., selective, raptorial capture of large algae cells by calanoid copepods).

Another area for model improvement would be in the representation of the winter biology of grazing zooplankters. We have ignored winter decreases in metabolism/mortality that at least

the copepods are likely to exhibit, and we have represented the effects of overwintering strategies such as resting eggs and benthic residence in a very weak way.

Energetics and Population Dynamics

Mysis relicta Energetics and Population Dynamics

Diel vertical migration by *Mysis relicta* prevents significant losses to kokanee or Gerrard predation in Kootenay Lake. Instead, *Mysis* interacts with the Kootenay Lake pelagic fish community indirectly, competing with kokanee for the grazing zooplankton as a food resource. Thus the focus of the *Mysis* submodel is the prediction of seasonal grazing zooplankton mortalities generated by *Mysis* predation.

Mysis' life history is geographically variable and may reflect lake productivity (Morgan 1980). In Kootenay Lake the life cycle is two years in duration. The model assumes an even sex ratio; eggs are deposited to the brood pouch of mature females in October of the second year of life. Fecundity is based on body size in the month of egg deposition. The mass of the predicted number of eggs is subtracted from mature female body mass at egg deposition. Immature individuals are released at a fixed body size in May of the following year. The model assumes that complete post-reproductive mortality occurs in May for both sexes.

The *Mysis* population is represented as numbers of adults and immatures per cubic meter of a 20 m epilimnion, averaged over the entire lake area. *Mysis* is modelled as an obligate zooplanktivore. All ages spend daylight hours inactive in the hypolimnion and night hours feeding in the epilimnion, minus a fixed time daily ascending from and descending to the hypolimnion. Nightly feeding forays occur year-round; surface temperatures in Kootenay Lake are never so high as to exclude *Mysis*, which are therefore assumed to be distributed evenly throughout the upper 20 m of the water column while feeding. Seasonal changes in nightlength are used to calculate the total monthly hours spent in the epilimnion.

Mysis are assumed to forage at a swimming speed of one body length per second, sweeping a cylindrical volume of water with radius set by the reactive distance, which is fixed for each life-stage. Consumption of prey types (copepods and cladocera) is determined using the Holling multi-species disk equation, where each prey type has a capture probability fixed for that prey type and Mysid life-stage. Handling time for each prey type, which includes digestive pause, is a function of *Mysis* body length.

Metabolism is calculated as a function of body weight and temperature. Since hypolimnetic and epilimnetic temperature are substantially different during part of the year, the model

determines total metabolic loss as a time-weighted sum of metabolism at the two temperatures. Specific dynamic action (metabolism associated with feeding), excretion, egestion and molting losses are calculated as a fixed proportion of food intake. Monthly growth or shrinkage is then the difference between assimilated mass and total metabolic costs.

Each life-stage is assigned a fixed baseline monthly mortality, which includes loss to outflow and predation. This can be adjusted to simulate increased predation losses. Management options which would result in additional loss of Mysis to the lake outflow can be simulated by increasing the proportion of time vulnerable to entrainment.

Predictions and Sensitivities to Parameters

The model reproduces the increase in Mysis abundance from first observation in Kootenay Lake around 1960 through peak abundance in the early 1980's, followed by a levelling off or possible slight decline through 1989. As currently parameterized, the model does not capture year-to-year fluctuations in abundance which appear in the historical time series. The basic prediction from simulations at high nutrient loadings (simulated fertilization) is that kokanee populations are outcompeted even more rapidly and additional production ends up in mysid biomass. Note that this result is more extreme than that found at Kennedy Lake where both mysids and fish have apparently increased under fertilization (K. Hyatt and K. Cooper pers. comm. 1991).

Overall growth in body size over the two year lifespan appears to be represented reasonably well. However, there are no data available to judge whether (1) growth is being properly distributed seasonally, and (2) mysid growth and fecundity are lower in years when mysid abundance is high and zooplankton abundance is low.

Uncertainties and Alternative Hypotheses

Nighttime hauls with a large mesh meter-square plankton net in Kootenay Lake captured about twice as many mysids as daytime standard plankton hauls made during the same time period (E.Parkinson, unpublished data). This suggests that the historical data which the model is currently parameterized to fit, may in fact substantially underestimate Mysis numbers in the lake. Initializing the model with higher mysid densities so that the population builds to roughly double the time series data, causes inter-year fluctuations in mysid numbers similar to those of the observed time series. However, the fluctuations are driven by poor growth and fecundity of Mysis due to impact on the grazing zooplankton community. The model kokanee population is unable to persist in the face of this increased competition.

Another possible uncertainty in the Mysis submodel is the importance of alternate food sources in the mysid diet. Mysids are also known to graze phytoplankton and consume detritus. However, conversion efficiencies for such food types would likely be much lower than for zooplankton prey. The metabolic coefficients, feeding rates and capture probabilities used by the model are based on extensive experimental work (Lasenby and Furst 1981; Ramcharan et al. 1985; Rudstam 1989). We are relatively confident that Kootenay Lake mysids must have been primarily zooplanktivorous in order to attain the overall growth rates which were observed in the late 1970's, when Mysid body length data was briefly collected.

Suggestions for Model Improvement

Major uncertainties about the Mysis-zooplankton interaction must be resolved before any meaningful improvements in the Mysis submodel can be made. A field monitoring program intended to evaluate the effects of lake fertilization should focus on obtaining adequate population estimates. In addition, seasonal body size data and fecundities are needed to evaluate whether size-fecundity or condition-fecundity feedbacks are influencing (1) Mysis population dynamics in the lake, and (2) seasonal grazing zooplankton mortalities exerted by Mysis.

The model fails to represent mysid flexibility in life history, thus predicting that at very low nutrient loadings kokanee are able to outcompete a mysid population with a fixed two year life-span. In reality, mysids may delay maturity to partially circumvent the body size-fecundity feedback. Age and growth data are needed to determine whether changes in lifespan may be important in determining mysid response to differing nutrient loadings.

Kokanee Energetics and Population Dynamics

The goal in the kokanee submodel is to mimic responses of the kokanee population to the numerous perturbations which have occurred over the past 30 years. The kokanee calculations are straight forward; kokanee growth is a function of zooplankton density, and predation on the kokanee is a function of the Gerrard rainbow population. Monthly zooplankton densities are obtained from the grazing zooplankton and Mysis submodels. Kokanee predation rates are returned to the plankton submodels. Kokanee densities are passed to the Gerrard model and densities after predation are returned. The time step of one month provided adequate resolution to capture seasonal effects such as photoperiod regimes for feeding, variation in trout food demand, and variation in prey densities.

The three north arm stocks (Lardeau, Duncan, and Meadow Creek) were represented in the model. Using empirical data from Bull (1965), initial (1960) escapements and juvenile carrying capacities

for each of the stocks were estimated. The model accounts for habitat loss due to the construction of the Duncan dam and the increased egg to fry survival resulting from the construction of the Meadow Creek spawning channel.

Functional Relationships and Limiting Factors

The seasonal dynamics are tightly coupled with the dynamics of the zooplankton. Seasonal changes in zooplankton density influence the growth of the kokanee. Feeding of the kokanee is modeled using the multi-species disk equation, which is a type II functional response model. For each kokanee age class (4), and zooplankton type (4), the feeding rate is predicted as follows:

$$c=((kvol*vul*zden)*tottime)/(1+handle*sumkvolvulzden)$$

where c = zooplankton eaten, kvol = the volume searched by a kokanee per hour, vul = the vulnerability of each zooplankton type to predation, tottime = total number of hours spent foraging per month, handle = total number of zooplankton eaten at high zooplankton densities, and "sumvolvulzden" is the sum over all prey types of the products kvol*vul*zden.

To account for the diurnal migration exhibited by kokanee in their first year of life, age 1 fish are limited to 30 hours of feeding per month (tottime=1 hour of feeding per day). Older fish are allowed a number of hours per day equal to the mean photoperiod for each month.

Growth and metabolism are modeled as a function of prey consumption. The "Wisconsin" metabolism model (Stewart et al. 1983) is the same for both kokanee and Gerrards (see Gerrard submodel) and includes temperature specific respiration and a constant loss due to feces and urine.

Growth for any month is calculated as:

$$growth= kwaste * contotwt - krespiration$$

where kwaste = proportion lost to feces and urine, contotwt = total weight of food consumed. The term krespiration is modeled as follows:

$$krespiration = ka * kwt \wedge kb * exp(ktdep * temp) * exp(kactivity * klen)$$

where ka,kb,ktdep, and kactivity are constants obtained from empirical data (Hewett and Johnson 1987), kwt = kokanee weight, temp = average monthly temperature, and klen = kokanee length.

A length-fecundity relationship was obtained from empirical data (Hutchinson 1986) and was represented by the following regression:

$$\text{eggs/female} = \text{kfslope} * \text{klen}(4) - \text{kfint}$$

where klen(4) = the length of age 4 fish, kfslope = the slope of the regression line, and kfint = the intercept of the regression line. Eggs per female times females (0.5 times number of age 4 fish) gives total egg production each year for each of the three stocks simulated.

The number of fry produced from the eggs laid each year is assumed to be controlled by two factors. First, an egg-to-fry survival rate (efs) is set for both natural and enhanced systems. efs is set at 0.05 for natural systems and 0.2 for the Meadow creek spawning channel. Second, a carrying capacity of each spawning grounds is also imposed. This capacity is represented with a Beverton and Holt stock recruitment curve:

$$\text{kfry} = \text{fry} / (1 + \text{fry} / \text{carrying capacity})$$

where fry=eggs*efs, and kfry is the final number of fry recruiting to the lake in May of the year following spawning. The carrying capacity for each stock is arbitrarily set at a level 25% higher than observed historic values.

Natural mortality (beside Gerrard predation) is treated as a constant low monthly mortality rate throughout the simulation. The rate is set higher for the first age of lake residence than for later ages.

Predictions and Sensitivity to Parameters

The kokanee submodel appears to track the historic information quite well. This historic information dates back to 1964, at least for the Meadow creek spawning channel. Meadow creek currently accounts for 60% of the spawning stock of Kootenay Lake. The model mimics this observation with considerable accuracy, by first predicting rapid declines in the other (wild) stocks and finally decline in the enhanced stock.

The overall prediction of the model is a decline in kokanee numbers. This is a result of two factors, competition by Mysis and predation by Gerrards. The Mysis are able to out-compete the kokanee for the zooplankton food resource while absolute Mysis numbers are increasing rapidly. This competition results in decreased zooplankton consumption, decreased growth rates and decreased size at age. This decreased size results in increased vulnerability to predation by Gerrards and the observed depensatory decline in kokanee numbers.

The model does not predict that fertilization will have a positive effect on the problems faced by the kokanee. The most dramatic remedial action for the kokanee would be reduction of Mysis, but a realistic method of reducing them has not been proposed.

One parameter to which the model is very sensitive is the egg-to-fry survival rate. If this rate is too high, the kokanee population remains stable regardless of the perturbations. If the rate is too low the population crashes. The values used in the final working model were obtained by consensus of the kokanee biologists present at the workshop.

Uncertainties and Alternative Hypotheses

The greatest uncertainty in the kokanee submodel is the slope of the type II functional response used in feeding rate predictions from food densities. The two components which can be altered in the disk equation are handling time and the rate of effective search. The response slope is the rate of effective search times total time available for feeding. The term labelled "handling time" accounts for the maximum number of prey eaten per kokanee at high zooplankton densities, and the model is not particularly sensitive to this parameter. By observing growth rates at various zooplankton densities, we can calculate an acceptable handling time.

The rate of effective search was not as easy to determine. The rate of effective search contains two parameters, prey vulnerability and search volume. The prey vulnerabilities for each zooplankton type were obtained from kokanee biologists as "best guesses". Using these estimates of vulnerabilities, the search volume was "fitted" to obtain growth rates similar to the observed data. In this fitting, we noticed that it is critically important what is assumed about kokanee feeding rate on Mysis. It is not known when or to what extent kokanee feed on Mysis. Anecdotal evidence suggests kokanee occasionally feed on it, but these events are not frequent enough to consider kokanee an important predator of Mysis.

Suggestions for Model Improvement

Better understanding of the predator-prey relationships of the kokanee would be useful. Actual, or more accurate, vulnerabilities of the prey items to the four kokanee age classes may be available from the literature. Little is known about the feeding behaviour of the older age classes of kokanee. The model assumes the kokanee spend all daylight hours feeding in the epilimnion. It is during this time the kokanee are vulnerable to predation. If the feeding behaviour of the kokanee is more complex, such as diurnal migrations once satiation has occurred, their vulnerability could be reduced. It was the opinion of the kokanee biologists present

at the workshop that the possibility of behavioral reduction of vulnerabilities exists but the kokanee do not have a refugia from predation. If this is true, reduced vulnerabilities may delay the kokanee population crash but it would not change the general predictions of the model.

Another improvement would be to represent the length-weight relationship of the kokanee as something other than allometric. The way the model is currently set up, kokanee lose length when food shortages result in decreasing weight. The model should decrease condition factor with decreasing weight, while conserving past length gains. This would improve the assessment of size-dependent mortality rates due to Gerrard predation, and give the kokanee a quicker simulated response to increases in zooplankton abundance.

Gerrard Trout Energetics and Population Dynamics

The basic objectives of the Gerrard trout submodel are: (1) to predict the impact of variation in density and size of kokanee on Gerrard trout growth and abundance, (2) to predict the age specific mortality schedule for kokanee due to Gerrard trout predation and (3) to predict the impact of exploitation on predictions (1) and (2). The spatial scale for the Gerrard trout submodel is the whole lake.

Inputs to the submodel include temperature, daylength and kokanee density and size by age at a monthly time step. Output from the submodel to the kokanee submodel is monthly kokanee age specific predation mortality. The Gerrard trout submodel calculates age specific growth and mortality for Gerrard trout at a monthly time step and annual reproduction and graduation to subsequent age classes.

Functional Relationships and Limiting Factors

The Gerrard trout population is made up of 10 age classes (0+ to 9+). They mature in May of their 5+ year and spawn annually including their 9+ year at which point mortality is assumed to be complete. The mature age classes feed exclusively on kokanee. The 3+ and 4+ age classes feed on a combination of littoral zone invertebrates and small kokanee. The feeding ecology of 0+, 1+, and 2+ is not modelled explicitly and they recruit into age 3+ at a constant body weight of 400 g. The number of 3+ juveniles that recruit into the population is based on body size/fecundity relationships (Andrusak and Brown 1986) and the assumption that egg to age 3+ survival is density dependent with maximum survival at low egg density and no additional 3+ production for egg deposition greater than 60,000 eggs.

This relationship produces a maximum recruitment of 10,000 age 3+ Gerrard trout which has been calculated as reasonable (Andrusak

and Brown 1986). This estimate of 10,000 3+ fish represents the maximum spawning capacity of the Gerrard trout spawning beds. Age specific natural and fishing mortality were chosen to approximate those estimated by Andrusak and Brown (1986), and reliably reproduce the age structure of adult Gerrard trout on the spawning grounds as estimated. Annual mortality rates were distributed evenly throughout months.

Consumption rates of Gerrard trout age classes are a function of the densities and size-dependent vulnerabilities of the kokanee age classes. The relative proportion of kokanee age classes consumed by Gerrard trout is calculated using the multispecies disc equation:

$$con_{ij} = \frac{sv_i * totaltime * vul_{ij} * pcap * den_j}{\sum_{j=1}^{n} sv_i * vul_{ij} * pcap * den_j * handle_{ij}}$$

and

$$svi = rd^2 * ss * len_i$$

and

$$totaltime = 30 * daylength$$

where con_{ij} is the monthly consumption rate in numbers of kokanee age classes j by Gerrard trout of age class i; sv_i is the search volume of Gerrard trout age class i in m^3/month; total time is the number of hours of daylight per month; vul_{ij} is the relative vulnerability of kokanee age class j to predation by Gerrard trout age class i; pcap is the probability of capture of prey within the search volume of the predator; den_j is the density of kokanee age class j in numbers per m^2; $handle_{ij}$ is the handling time for predator i feeding on prey j in hours; rd is the reactive distance of Gerrard trout in m; ss is swimming speed in body lengths per hour; len_i is length in meters of the predator and daylength is the number of daylight hours per day.

Vulnerabilities (vul_{ij}) to successful attack for combinations of Gerrard trout and kokanee age classes were assumed to be size-dependent. We assumed that Gerrard trout do not begin feeding on kokanee until the kokanee are at least 10% of the Gerrard length. This approximates the observation that adult Gerrard trout rarely feed on 0+ kokanee which are less than this 10% prey:predator length ratio. We assumed that vulnerability for ratios of prey to predator length of 10 - 20% are maximum and that Gerrard trout cannot capture and ingest kokanee larger than 30% of their length. Vulnerability for prey between 20 and 30% of their length were assumed to follow a decreasing linear function from maximum vulnerability at 20% to 0% vulnerable at 30% of predator length. Once the vulnerability to successful attack is calculated for combinations of Gerrard trout and kokanee age classes it is assumed that the Gerrard trout would successfully ingest prey on 10% of the attacks.

Once monthly consumption rates are calculated, the resultant monthly growth rates are calculated assuming a simple energy budget which has been examined in detail in the literature for salmonids by Stewart et al. (1983) and Hewett and Johnson (1987):

growth = consumption - (waste losses + metabolic costs)

where waste losses are a constant proportion of consumption and metabolic costs are body size, temperature and swimming speed dependent. This general approach is successful at approximating growth trajectories for mature Gerrard trout during the spring, summer and fall. Extrapolation of the well known allometry and temperature dependence relationships to small body sizes and the low temperatures experienced during the winter produced unrealistic growth patterns. We therefore tuned these relationships to best reproduce observed seasonal growth of adults and we did not explicitly model growth of Gerrard trout less than 400 g.

Predictions and Sensitivity to Parameters

The Gerrard trout submodel predicts well the interannual average number of spawning Gerrard trout as observed on the spawning beds. It does not capture the observed year to year fluctuations in spawner density, but rather produces a stable density and age distribution of mature Gerrard trout. This result is due to having in the model a constant age specific mortality pattern throughout the 30 years of the simulation. Unfortunately there are not adequate data available to determine temporal trends in age-specific mortality rates, even though they have certainly changed through the period 1960-1989. The Gerrard trout submodel also predicts well the age-and size-dependent growth rates of the Gerrard trout and produces reasonable predation mortality rates for the kokanee age classes.

A consistent prediction from the Gerrard trout submodel that is rather disconcerting from a management point of view is that the very efficient search and capture behaviour of the Gerrard trout is able to exert depensatory mortality on the kokanee population. This means that once the kokanee population declined to the densities and growth rates observed in the 1980's, no management initiatives short of elimination of Gerrard trout are sufficient to prevent the kokanee population from going extinct. The precision of the timing of this prediction can be questioned but it is reasonably clear that it will happen within the next decade (for qualifications of this assessment see next section).

The Gerrard trout abundance and size and the kokanee predation mortality schedule is insensitive to the parameters in the feeding subroutine. Although initially somewhat counterintuitive, the reason for this insensitivity is that the Gerrard trout feed at near maximal rates at all kokanee densities modeled. This means that Gerrard trout are very efficient predators and are not limited

in their feeding by kokanee density but rather by the time it takes to evacuate ingested prey. Therefore changes in parameters associated with search rates, swimming speed, vulnerability and probability of capture will have little influence on predictions.

On the other hand, predictions are quite sensitive to evacuation rates. We therefore carefully tuned this parameter to produce the consumption rates observed in the field of 1-2 kokanee eaten per Gerrard trout per day (Harvey Andrusak and Eric Parkinson, personal observation). The Gerrard trout submodel predictions were also quite sensitive to the assumed stream carrying capacity for juvenile Gerrard trout which we set at 10,000 age 3+ which was reported by Andrusak and Brown (1986) after substantial statistical hoochery and diddling. This is clearly an area that requires empirical research if we are to understand the population dynamics of the Gerrard trout.

Uncertainties and Alternative Hypotheses

As flagged in the previous section, the most important uncertainty in the Gerrard trout submodel is the stream carrying capacity to produce juvenile Gerrard trout. Evidence of early stream and lake distribution, feeding, growth and mortality are largely anecdotal, and we have chosen to model the net result of these processes in terms of an overall input-output relationship. We have therefore adopted the assumption that egg to 3+ survival is density dependent and size at recruitment is constant.

A second uncertainty that we have not yet made any attempt to remedy is the assumed tight coupling of Gerrard trout consumption and kokanee mortality. In Kootenay Lake there are other kokanee predators (i.e., burbot, Slimelinus) and other potential Gerrard trout prey (small trout, littoral fishes). It is not clear from the empirical work that has been done in Kootenay Lake what the impact is of these additional kokanee predators or whether the Gerrard trout may be able to switch to alternate prey as the kokanee abundance declines, thereby providing the kokanee a refuge from extinction.

Suggestions for Model Improvement

One key area for improvement in the Gerrard trout submodel is in the representation of the early life history. It may be that there is sufficient information in the literature from other rainbow trout populations to do a more credible job of modelling the first 3 years of life. A second important area for improvement is our representation of the management actions of harvesting and stocking. There may be more specific information available on the management of the Gerrard trout stock over the 1960 to 1989 period. Adding these temporal patterns as input to the model may improve the fit of predicted to observed spawning counts.

A third area for improving the model is in the representation of metabolism, of small Gerrard trout and of large trout at winter temperatures. Both of these processes are general problems in our understanding of fish bioenergetics at the extremes of body size and temperature (Post 1990; Post and Evans 1989).

MODEL USERS GUIDE

This section is intended to provide a brief overview of how to run the program, set graphics display options, and make changes in model parameter and policy options. Here we do not attempt to describe every parameter and option in detail; the effects of most parameters are most easily discovered by the model user simply by varying them and seeing what happens. Questions concerning specific parameters should be directed to the authors. **In using the data file saving options in the program, care should be taken to avoid specifying the data file prefix "kootnay", since that may cause the program to overwrite key data files provided with it.**

Loading the Program and Data Files on Your System

The model is provided as a series of program and data files beginning with the DOS file prefixes "kootnay" and "kootnayu". File extensions .BAS and .EXE denote programs, while files with other extensions (.HIS, .MPD, .KOK, etc.) contain historical data, and parameters stored in standard ASCII format. To set up the program on your hard drive, simply type "copy b:kootnay.*" and "copy b:kootnayu.*" when you are in the directory where you want the files to reside and you have put a diskette containing the model in drive b:.

Note that to run the program from your hard drive, you will need to have at least 200 kb of disk space free besides the space taken by the program and data files (approximately 400 kb). The extra space is used by the program for temporary storage of graphics results (in files called SCR.ext) when you intervene during a simulation. If you want to run the provided QuickBasic version of the program as well as the compiled version (necessary only if you want to make changes in the program), note that you will also have to have Microsoft's QB.EXE version 4.0 or higher on your disk, either in the same directory as the model or accessed via a PATH command to the directory where it resides. You should avoid using the QuickBasic version except when necessary, since it is much slower to run and can be inadvertently damaged in various ways if you are not familiar with the QuickBasic user interface and editor.

Running the Program and Accessing Menu Items

To run the model after its files are loaded on your disk (or from the diskette provided), just type "kootnay". To run the slower QuickBasic version, type "qb kootnay" then hit the shift and

F5 keys simultaneously after the QuickBasic interface is finished loading the program (see caution above about running the QuickBasic version). The program should display the message "Loading data, please wait..." as soon as it is loaded and begins execution. Then the screen should clear and you should see a menu of choices with the first item highlighted ("set gerrard population parameters").

FOR THIS AND ALL OTHER MENUS PRESENTED BY THE PROGRAM, MOVE AMONG CHOICES BY HITTING THE UP AND DOWN ARROW KEYS, THEN MAKE A SELECTION BY HITTING THE ESC KEY.

You can now begin a simulation run with default parameter values and graphics configuration by selecting the "simulate dynamics" option. Selecting options related to model parameters will send you to other submenus that allow you to edit parameter values and save/restore parameter values from files. After making as many such changes as you want, you can begin a simulation at any time by selecting the "simulate dynamics" option.

However, note that you will generally not want to make changes initially in policy-related parameters (fertilization, fish management), since these will be applied over the whole simulation base period (1960-90) as well as any future years; it is better to wait until later in the simulation to make management-related interventions (though you can, of course, ask questions of the form "what does the model predict would have happened if we had done X in 1960").

Selecting Graphics Display Options and Simulation Term

At the beginning of each simulation run (if you have not elected to overlay results from the last run made), you may use the menu choice "select graphics options, simulation time" to make changes in the total number of years to simulate and in the arrangement of graph "panes" used to display predictions over time as the simulation proceeds. After selecting this choice (highlight by using up/down arrow keys, hit esc), the screen should clear and you should see a crude "spreadsheet" divided into three sections.

The top section of the spreadsheet (first 25 rows) lists various "graph panes" that show interannual variation in model predictions and historical data. To have any of these displayed during a simulation (up to 16 can be shown at once, though you will not have so many choices in this model), use the up/down arrow keys to move the highlight to the box next to the panel's title, then hit the "x" key to turn on the panel. To turn off a panel, highlight the box next to its title, then hit the space bar.

The middle section of the spreadsheet is a four-line list of options for plotting monthly body size/abundance time series across the bottom of the computer display screen. Use the up/down arrow

keys to highlight the single digit choice number on the first line of this section, then type a single digit number (0,1,2) to make your choice. Note that all the choices give a monthly plot of kokanee body lengths and numbers by age class; what you can choose is whether to also plot Gerrard lengths/numbers by age, copepod and cladoceran monthly biomasses, or Mysis body lengths and numbers.

At the bottom of the spreadsheet is a two digit number (use arrow keys to move down the page to highlight it) giving the number of years to simulate, beginning 1960. It is set by default to 30 (i.e., 1960-89). You can overtype this number with a number as large as 50 (or as small as 2). Setting numbers above 50 (to year 2010) will have no effect, since the program does not store time series nutrient loading values (which you can set in another spreadsheet) beyond that time. If for some reason you need to make longer runs, contact the authors for information about how to change the program to do so.

Interpreting the Graphics Display During a Simulation

While a simulation run is in progress, the computer screen will display a number of graph panels or boxes or "panes". Think of each of these as a time series plot, with time on the horizontal or X axis of the pane. The panels are arranged in three general groups. At the top left of the screen, three panels are used to draw simple maps of the lake with colour codes to indicate the spatial distribution along the lake of simulated zooplankton, surface phosphorus concentration, and deep water phosphorus concentration. The colours shade from light blue for very low concentrations, up through green and yellow, to red for very high concentrations. In particular, red for the phosphorus maps designates total P concentrations above 60 μg/L; red for the zooplankton denotes dry weight biomass above 0.5 mg/L.

The top right side of the screen shows one or more graph panes showing annual values of variables (such as surface water P concentration in March at three stations, from north to south along the lake). For the fish and Mysis variables, the values plotted of numbers and body lengths are the simulation results for the end of December, except as noted in the panel titles. Measured values of variables (from the kootnay.his data file) for 1972-89 are shown for some cases, always as dots or circles without lines connecting them.

Making Changes in Parameters and Policies

Before and during simulation runs, you can access menus and spreadsheets to make changes in and save/restore filed values of parameters and policy variables. Note that whenever you make a change in a numerical quantity, that change remains in effect over all simulation years **and all subsequent simulation runs** while the program is still executing. If you make a lot of changes and have become confused about which ones are still in effect, you should

stop the program ("quit" option in menus) and run it again by typing "kootnay"--that will restore all the parameter values from the default data files beginning with "kootnay." prefixes.

To change parameters for one of the submodels, select the appropriate submodel from the main menu description (highlight description, hit esc). Then a sub-menu should appear with choices to return to main menu, edit parameter values, and save/restore values from file. Select (arrow keys, esc) the edit parameter values option. A crude spreadsheet should then appear on the screen, with bits of descriptive text and associated numerical values. To edit any numerical value in the spreadsheet, use the arrow (up, down, left, right), tab, and backspace keys to move the highlight to the field containing the value. Then simply overtype the value with whatever new one you want to try. Be careful here to do the overtyping so as not to leave any extra decimal points, blanks, or alphabetic characters. If you are not sure whether you have typed a value correctly, exit the spreadsheet by hitting esc and select the edit choice again. The spreadsheet will come up a second time (or as many times as you like), and you can look to see what values are in the fields that you just edited.

When you are finished editing the values in a spreadsheet, you return to the menu system by hitting the esc key. Hitting the esc key twice moves you back from the spreadsheet to the menu for the particular parameter group that you are editing, and from there back to the main simulation control menu. Hitting it once gets you just back to the sub-menu where you can make choices about whether to save the edited values in a file for future use. Note here that you can also use the restore option to read back in a file of values that have been stored earlier, but doing this after editing will cause the edited values to be overwritten with whatever values are in the file that you restore.

When you save/restore parameter values from files using the sub-menu save and restore options, the program will ask you to specify a file prefix to use. The program then saves the parameters under a file name it creates by using your prefix plus an extension that depends on what type of parameters you are editing (.KOK added for kokanee parameters, .GIR for trout, etc.). These files are then permanently available on your disk, unless you overwrite them with new values or deliberately delete them from DOS. As noted above, be careful not to use the prefix "kootnay" unless you want to overwrite the default parameter values used every time the program is started. Also, be careful that your prefix names do not contain more than 8 letters, and that they do not contain any blanks. If you use a prefix like "my value" with a blank in it, you will likely be unable to even delete the file from your disk, let alone have the program read it later (DOS is really stupid that way).

Changing Fertilization and Water Flow Regimes

Here you may need to use two of the menu options: "set primary production parameters" and/or "edit lake maps". You set amounts of fertilizer to add by month, and/or river input concentrations, in the primary production parameters spreadsheet.

The edit lake maps option allows you to put up a small map of the lake on the screen (choose "fertilization sites" map to edit), and you can select which 2000 ha model grid cells to fertilize by setting the map code numbers for those cells to 1 (default is all cells set to 1). To avoid fertilizing a cell, set its fertilization site map value to 0.

To set amounts of fertilizer to add to the fertilized cells, select the "edit primary production parameters" menu choice and select "edit parameters". A complex spreadsheet should appear. This spreadsheet is divided into three parts: (1) a table specifying overall and monthly relative values for various parameters; (2) a block of inputs for the Duncan River, allowing you to set its water regulation schedule (natural or managed) by year, mean P loading, and relative loading by year for 1960-2010; and (3) a block of inputs for the Kootenai River, set up as for the Duncan River. Make changes as appropriate, and hit esc to exit the spreadsheet.

Partway down the first spreadsheet table is a row for fertilizer additions. Here you can set the amount of fertilizer to add to each active cell each month ($g/m^2/mo$), and relative additions for each month of the year. A relative loading of 1.0 means fertilize the cell, and 0.0 means do not fertilize for that month; values between 0 and 1 can be used to set partial loadings for particular months. If you want to simulate changes in P loadings for the Duncan or Kootenai Rivers, be careful how you make the changes in the spreadsheet block. You can change either the overall mean P concentration for the river, or the relative concentration for particular years (concentration in model will be the overall times the relative value for the year), or both. It is a good idea to just change the relative concentrations by year, since the overall value will be applied to all years in the simulated time series.

Changing Mysis Mortality Rates

Enter the Mysis parameters spreadsheet. About half-way down the parameter list, you will see monthly natural mortality rates for ages 1 and 2+ Mysis. These can be overtyped to simulate introduction of a predator. Hit esc to exit the spreadsheet.

Near the bottom of the spreadsheet is an entry for the proportion of Mysis vulnerable to export over the West Arm sill. This is the proportion of the Mysis that will be subject to the surface water volume exchange rate over the sill (averages around

0.2/mo). A passively moving Mysis spending 30% of its time in the lake surface waters would have an export vulnerability parameter of 0.3.

Changing Kokanee Reproduction and Harvest

Enter the kokanee parameters spreadsheet. You will see lines and numerical fields for egg/fry survival rates, fry carrying capacities by stock, and annual harvest rates by age of kokanee. Overtype the appropriate parameters with new policy values, and hit esc to exit the spreadsheet.

Changing Gerrard Reproduction and Harvest

Enter the Gerrard parameters spreadsheet. Here you will see an entry (text line, numerical field) for juvenile carrying capacity, and entries for harvest rates. Overtype the appropriate parameters with new policy values, and hit esc to exit the spreadsheet.

Intervening During Simulation Runs

You can stop the simulation at any simulation year (calendar year is displayed in the top right corner of the computer screen while the model is running) just by touching any key once. At the beginning of the simulation year after you touch a key, the program will pause and print a flashing "holding" message at the bottom of the screen. Then just touch any key once. The computer will then dump the graphics display to disk, and put up a menu of intervention choices involving the same parameter menus that appear at the start of a run. You can now edit parameter values, save/restore parameters to files, or quit the program entirely.

When you select the "continue simulation" option from the intervention menu, the graphics screen will be restored from diskette (this fails on certain PC clones) and the simulation will proceed from where it left off. Note that while you can make various parameter changes and these will come into effect immediately (in the simulation year where you stopped), you cannot save/restore a whole new set of values of the model state or internal variables (e.g., state for some different calendar year or from some other model run); the model has too many variables to make such a save/restore option practicable to program.

Options at the End of a Simulation: Saving Graphics Results and Overlaying Results of Successive Runs

At the end of each simulation run, a simple menu will appear that allows you to save the final graphics display (results of all years), return to the main menu, or immediately begin a new simulation run without returning to the menu. If you want to begin a new run immediately, you can elect to do that with either a fresh graph screen (results of last run erased), or with the previous

results left on the screen.

If you elect to start a new run with the previous results left on the screen, the program will plot some of the new run's results with small boxes overlaying the time series lines, so that you can compare the new results to previous ones more easily. Note that once you choose the "overlay results" option, it will remain in effect over successive simulation runs even if you return to the main menu at some point, until you elect to start a new run with a fresh screen. Any successive overlays will be plotted with the same box character as the first one, so the screen will soon become hopelessly cluttered.

KEY UNCERTAINTIES IN MODEL PREDICTIONS OF RESPONSE TO FERTILIZATION

The model essentially traces impacts of fertilization through the pelagic food web. While there is some uncertainty about the physics and chemistry of phosphorus movement in the system, this uncertainty is small in comparison to uncertainties concerning biological processes that transform changes in phosphorus concentration into eventual fish production via the food web. Key uncertainties about biological responses can be summarized as questions that arise about successive links in the food web:

(1) Will added phosphorus result in increased production by grazeable algae, or will increases instead be "shunted" into ungrazeable algal forms (large cells, colonies) that simply increase phosphorus loss rates from the epilimnion (via settling)?

(2) Are grazeable algal forms limited in production rate by phosphorus concentration in the first place, or instead by grazing rates and other factors?

(3) Are grazing zooplankton species that are usable by kokanee now limited by algal food availability and production, or instead by Mysis and fish predation (if predation is limiting, increased algal production will go only to grazing species that are not taken by fish)?

(4) Will increased production of grazing zooplankton be available to kokanee, or will this increase instead be taken up entirely in production of higher abundances of Mysis?

(5) If kokanee growth rates are increased by increased production of grazing zooplankton, will the kokanee become more or less vulnerable (or be vulnerable for longer or shorter times during their life cycle) to Gerrard predation (i.e., will the Gerrards initially benefit or suffer from increased kokanee growth rates)?

(6) Will improved kokanee growth/fecundity, and possibly survival, be adequate to overcome the depensatory effects of Gerrard predation, or are the kokanee stocks now so low that this predation

will continue to drive them down in spite of any improvements?

(7) Will fertilization effects on the benthic/littoral part of the lake ecosystem be beneficial or detrimental to Gerrard (and kokanee) production, or will fertilization instead enhance mainly competitors and predators?

These same uncertainties have plagued other lake fertilization programs (Stockner 1987), and there is as yet no definitive, empirical answer to any of them for lakes that are closely comparable to Kootenay. Based on past experience with Kootenay Lake, questions (1)-(3) are relatively minor concerns; historically there do appear to have been positive responses of grazing zooplankton to phosphorus loading, as evidenced by kokanee growth rates if not by changes in abundance of the most obvious food species (copepod and cladocerans).

RECOMMENDED RESEARCH PRIORITIES

The most important uncertainties today are represented by questions (3)-(6) in the section above. These involve predator-prey interactions that have been difficult to study in the field due to the relatively large space/time scales over which their effects are exhibited, and due to their cumulative nature (e.g., how do improved conditions for Mysis feeding eventually translate into changes in Mysis abundance via improvements in fecundity and survival?).

We believe that research in conjunction with a field fertilization trial should concentrate on monitoring three main responses:

(1) changes in size, density, and species composition of grazing zooplankters, especially during the early part of each growing season (spring);

(2) changes in Mysis growth, fecundity, and abundance, especially for small juveniles during summer and fall;

(3) changes in kokanee growth rates and size-selective mortality rates due to Gerrard predation, through seasonal sampling of kokanee densities and Gerrard stomach contents, along with techniques such as back-calculation of growth histories of surviving fish from scale/otolith characteristics.

Improved monitoring for (1) and (2) could be accomplished by relatively modest changes in existing programs, to sample Mysis using more representative gears/times and to provide more thorough laboratory processing of plankton samples. Improved monitoring for (3) would require a regular (i.e., monthly) netting program for kokanee, most likely using mid-water trawls operated to stratify for or minimize size-selectivity effects, along with substantial

laboratory effort for scale/otolith measurements. Synoptic limnology information (temperature, oxygen, N, P, chl a, phytoplankton composition) should also be gathered in conjunction with these monitoring programs.

Fertilization of only the North Arm should, based on model calculations, create a strong north-south gradient in primary productivity; this gradient should be exploited in monitoring grazing zooplankton responses, to provide within-year comparisons of seasonal patterns. However, it is likely that effects on Mysis and kokanee will be distributed throughout the Lake, due to their longer life cycles and active movements. Improved growth/survival of these species while resident in the North Arm may even result in negative effects on grazing zooplankton abundance in the South Arm, due to increased predation there by animals wandering from the North Arm.

There is one main conclusion from the modelling work. It will be expensive to fertilize the lake, and the uncertainties are great enough to imply that this expense should be matched by a substantial investment in monitoring and research to determine whether it is really working in both the short and long term.

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